Sex ratio of hatchling loggerhead sea turtles: data and estimates from a 5-year study

N. Mrosovsky

Departments of Zoology and Psychology, University of Toronto, Toronto, Ont.; Canada M5S 1A1

AND

Jane Provancha

The Bionetics Corporation, Kennedy Space Center, FL 32899, U.S.A.

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Hatchling loggerhead sea turtles (*Caretta caretta*) were collected over three nesting seasons from a rookery at Cape Canaveral, Florida. From data on the distribution of nests over the season, we estimated that 92.6–96.7, 94.7–99.9, and 87.0–89.0% of the hatchlings produced on this beach in 1986, 1987, and 1988, respectively, were females. These skewed sex ratios were consistent with the fact that for most of the season, sand temperatures were above the pivotal level for loggerhead turtles. The present results show that the female-biased sex ratio reported previously by these authors for the 1986 nesting season at this site was not an isolated, atypical event. In addition to a total of 3 years of sampling for sex ratio, measurements of beach temperatures at the depth of turtle nests were extended to cover 5 years. These temperatures were commonly above the pivotal level. The strongly female-biased hatchling sex ratio found in this population of loggerhead turtles poses theoretical challenges. It may also complicate conservation efforts, since global warming might be expected to skew the sex ratio still further toward females.

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De petites Caouanes (*Caretta caretta*) nouvellement écloses ont été récoltées au cours de trois saisons de nidification dans une rookerie du cap Canaveral en Floride. D'après les données recueillies sur la répartition des nids au cours d'une saison, nous avons pu estimer que 92,6–96,7 en 1986, 94,7–99,9 en 1987, et 87,0–89,0% en 1988, des tortues écloses sur cette plage étaient des femelles. Ces rapports mâles : femelles déséquilibrés s'expliquent par le fait que les températures du sable ont été au-dessus des températures de pivotement de cette espèce pendant presque toute la saison. Ces résultats indiquent que le nombre plus grand de femelles enregistré précédemment au cours de la saison de nidification de 1986 par ces auteurs à cet endroit n'est pas un phénomène atypique isolé. En plus d'avoir échantillonné des tortues pendant 3 ans dans le but d'établir le rapport mâles : femelles, nous avons mesuré les températures sur la plage à la profondeur des nids au cours d'une période de 5 ans. Ces températures étaient souvent au-dessus des températures de pivotement. Le rapport mâles : femelles fortement déséquilibré enregistré au moment de l'éclosion chez cette population de caouanes pose un problème théorique important; il peut aussi gêner les tentatives de conservation, puisque le réchauffement global risque de favoriser encore plus l'éclosion de femelles.

[Traduit par la rédaction]

Introduction

In many reptiles, sea turtles included, the direction of sexual differentiation of the embryo depends greatly on the temperature prevailing during incubation of the egg (Raynaud and Pieau 1985). In 1986, as part of an effort to discover the sex ratios that turtles produce in natural circumstances, we collected hatchling loggerhead sea turtles from Cape Canaveral, one of the major nesting beaches for this species in the United States. An extremely skewed sex ratio was found: it was estimated that 95% of the hatchlings produced were female (Mrosovsky and Provancha 1989).

Such a highly skewed ratio is surprising because according to Fisherian principles, when the costs for male and female embryos are similar, the sex ratio should be close to 1:1. One way out of this theoretical challenge would be to reject the 1986 loggerhead turtle data as atypical. Perhaps this was a thermally atypical year. Therefore, we extended our sampling of loggerhead hatchlings at Cape Canaveral for a further 2 years, 1987 and 1988. We also monitored the temperature at turtle nest depth for an additional 2 years, providing 5 years of sand temperatures, 1986–1990.

Materials and methods

Study area

The beach at Cape Canaveral Air Force Station, Florida, has been described previously (Provancha et al. 1984; Provancha and Ehrhart 1987; Mrosovsky and Provancha 1989). Hatchlings were collected from km 1 to 21, with >86% in each year coming from km 7 to 13. Because our focus was on natural sex ratios, no samples were collected from the very few areas shaded by exotic Australian pines; in any case these areas affected <1% of the nests.

Assignment of nests to sex-ratio sample

There were six sampling periods, each of a half-month duration, starting in the second half of May and ending after the first half of August. The beach was patrolled on several mornings during each sampling period, and the first few nests encountered were assigned to the sample. In 1987, the numbers of nests assigned in the six sampling periods were 20, 19, 18, 22, 19, and 11. In 1988, because heavily female-biased sex ratios had been found during July in previous years, no samples were collected during this month; instead, the sex ratio was estimated from sand temperatures. The numbers of nests assigned to the second half of May and to the first and second halves of June were 17, 21, and 18, respectively. No nests were assigned to the first half of August 1988. More nests than required

TABLE 1. Percentage of females in samples from different clutches and number of nests laid from May to September, 1986–1988

	May 1–16	May 17–31	June 1–15	June 16–30	July 1–16	July 17–31	Aug. 1–16	Aug. 17–31	Sept. 1–15
				1986[a]					
Mean % ♀		72.1	98.2	100	100	100	100		
Number of nests	24	267	543	517	516	447	136	68	12
% of nests laid	0.9	10.6	21.5	20.4	20.4	17.7	5.4	2.7	0.5
				1987					
% ♀ in clutch		100	100	100	100	100	100		
		100	100	100	100	100	100		
		100	100	100[b]	100	100	100		
		100	100	100	100	100	100		
		100	100[c]	100	100		100		
		100	100	100	100		100		
		100	100	100	100		100[c]		
		100	100	100	100		100		
		90							
Mean % ♀		98.9	100	100	100	100	100		
Number of nests	34	213	439	501	504	418	221	78	13
% of nests laid	1.4	8.8	18.1	20.7	20.8	17.3	9.1	3.2	0.5
				1988					
% ♀ in clutch		30	60	100		100			
		0	100	100		100			
		56[d,e]	30[e]	80					
		90[e]	50[e]	100					
		0	70	100					
		60	40	100					
		30	67[d,f]	100[d]					
		50	70	90[f]					
		100	100[c]	100					
			100						
Mean % ♀		46.2	68.7	96.7			100		
Number of nests	12	215	447	497	589	392	276	27	8
% of nests laid	0.5	8.7	18.1	20.2	23.9	16.0	11.2	1.1	0.3

NOTE: Clutches above short horizontal lines were from those originally designated for sample, those below line were added retrospectively. For all samples, $n = 10$ unless otherwise noted. Total number of nests was 2530 in 1986, 2421 in 1987, and 2463 in 1988. Wire screen was not used over nest except where noted.
[a] See Mrosovsky and Provancha (1989) for details of sample.
[b] Sample size 8.
[c] Late embryos from eggs sampled.
[d] Sample size 9.
[e] Wire screen over nest throughout (see Mrosovsky and Provancha 1989).
[f] Nonfemale animals include 1 intersex.

were designated in anticipation of some losses. Nevertheless, for some sampling periods it was still necessary to add nests retrospectively to the sample (Table 1). Except during the second half of July 1987, predation was not as heavy as in 1986 (Mrosovsky and Provancha 1989). A wire protection screen was not used over the nests in 1987 and 1988, except in a few instances noted in the results (Table 1).

Collection and sexing of hatchlings

A few days before estimated emergence, a chicken-wire trap was positioned around each clutch to capture the hatchlings. After emergence, hatchlings within the traps were stirred by hand. Ten animals were then rapidly collected from different parts of the mass of hatchlings. Occasionally it was not possible to select the final samples from the full complement of hatchlings (e.g., nest was partially destroyed by predators, some hatchlings emerged outside of the trap). Cases in which the attempted random selection of hatchlings was com-

promised are noted in Table 1. Sex was determined by microscopic examination of sections of the gonads (Mrosovsky et al. 1984a).

Seasonal nesting frequency

Data on nesting frequency came from the entire 33 km of the Cape Canaveral Air Force Station and Kennedy Space Center beaches (see map, Mrosovsky and Provancha 1989). These beaches were patrolled in 1986–1990 on almost every day of the nesting season. Systematic patrols started after informal observations of the first turtle crawls by personnel working on the beach for other reasons. Patrols ended in September after no nesting had occurred for 3 consecutive nights. It is possible that a few nests were missed at the beginning and end of the season, but the number was certainly low.

Sand temperatures: manual data collection

Temperatures at 30 and 60 cm depths were recorded about twice a week at 16:15 (±30 min) between May and October through YSI

ermistor probes. This time of day was chosen because it reflects mean temperature over 24 h (see below). The probes were buried along transects that were in approximately the same location each year, 10 km north of Port Canaveral. This particular section of the beach has high densities of nesting loggerheads each year (Provancha and Ehrhart 1987).

A transect comprised three stations spaced a few metres apart on the beach from the primary dune toward the sea. With few exceptions, each station had two probes attached to a stake, one buried at 30 cm and one at 60 cm depth. The most landward station ("high") was on fairly flat ground at the top of the primary dune, sometimes partly shaded by sea oats and railroad vine. The next station ("mid") was on an open seaward slope of the dune, while the third site ("low") was on the berm near the high-tide line. The stations proved to be representative of nest sites on several occasions when females dug up a probe while nesting. Two transects were used in 1987, 1988, and 1990, and one transect in 1986 and 1989, plus an extra-high beach station in 1986. During years when there were two transects, they were no more than 100 m apart. Because some probes did not pass quality control tests, the second transect in 1990 was not equipped with probes at the 60 cm depth.

The mean values for the readings from each probe for each half-month period were calculated. Values for probes at a given depth (30 or 60 cm) and a given location (high, mid, or low beach) were pooled. The YSI thermistor probes were calibrated against accurate mercury thermometers at the beginning and end of each season. The probe readings were accurate to $0.2-0.3°C$. The YSI meters were also calibrated every few weeks during the season.

Sand temperatures: automatic data collection

Over parts of each season, depending on availability of the equipment, temperatures were continuously recorded with data loggers. The three data loggers used over the 5-year period were the Hydrolab Datasonde (model 2020, accuracy $\pm0.1°C$), the Grant Squirrel Meter (accuracy $\pm0.2°C$), and the Li-Cor data logger (model 1000, accuracy $\pm0.5°C$). The units were buried at the 30 cm depth $\pm$ 8 cm, within 2 m of a midbeach station with thermistor probes.

The units were generally programmed to collect temperature readings every 2 h, but the specifications ranged between 1- and 4-h intervals, depending on battery constraints and equipment availability. Therefore, these recorders provided between 6 and 24 data points per 24-h period; means for each day were calculated from these points. Values for each half-month period were the means of the daily mean temperatures. The number of days per half-month for which information from data loggers was available averaged 8−12 in 1987−1990 and 4 in 1986. Unlike the other data loggers, which had detachable temperature probes with cables, the entire Hydrolab unit had to be buried at the specified depth. At least 8 h of data were excluded after burial of a data logger to allow for thermal equilibration. Data loggers were calibrated against an accurate mercury thermometer before and after use.

Sand temperatures: comparison of the two methods

For some of the half-month periods, data from a data logger were more extensive (taken round the clock and over more days) than those from the thermistors (taken at one time of day about twice a week). However, there were several thermistor probes at each depth, but only one data logger. In any case, the two methods of estimating seasonal changes in temperature agreed fairly well. This agreement depends on the choice of 16:15 ± 30 min for taking thermistor probe readings as a time of day when sand temperature is usually close to the 24-h average. This was checked previously (Mrosovsky and Provancha 1989), then more extensively in this study. Figure 1 presents an example of a comparison between temperatures at 16:00 and 24-h mean temperatures.

Results

Sex ratios in both years were highly skewed toward females. From the sex-ratio data for different half-month periods, and the seasonal nesting distributions (Table 1), it may be calcu-
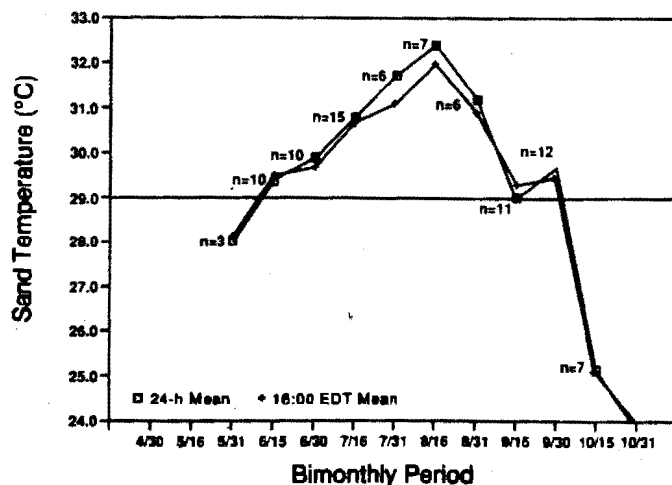

FIG. 1. Validation of 16:00 as a time when sand temperatures at 30 cm reflect the average temperature for a 24-h span. For each half-month period ending on the dates shown, the figure shows the mean (of *n* days) of the readings taken at 16:00 compared with mean of the 24-h means for the same days obtained from the same data logger. The latter recorded temperature continuously; for this graph readings taken every 1 h were used to provide a mean for each 24-h span.

lated that >94% of the hatchlings produced in 1987 and >87% of those produced in 1988 were females. The calculations for 1988 assume that the hatchlings produced in July were all females; this is reasonable given that high percentages of females were found in adjacent months and that sand temperatures in July 1988 were above the pivotal temperature (Figs. 2 and 3).

A few nests were laid outside of the periods when hatchlings were collected for the sex-ratio samples (Table 1). If it is assumed that all these nests produced males only, then in 1986, 1987, and 1988, females still constituted 92.6, 94.7, and 87.0% of the total hatchlings. If it is assumed that all these nests produced females only, then 96.7, 99.9, and 89.0% of the hatchlings in these years were females. That the differences in the estimates arising from these opposite assumptions were so small reflects the fact that few turtles nested during the periods at the beginning and end of the season when samples for sex ratios were not collected. The very small differences in the 1986 estimates given by Mrosovsky and Provancha (1989) arise from the few turtles nesting in the first half of May not having been included in their calculations. Whatever the exact figures, it is clear that in all 3 years far more females than males were produced.

The high percentages of females are consistent with the fact that sand temperatures were usually above the pivotal level of 29°C for loggerheads in the southeastern U.S.A. (Figs. 2 and 3). The greater number of males produced in early 1988 compared with 1986 and 1987 (Table 1) is consistent with the fact that sand temperatures rose relatively slowly in 1988 (Fig. 4).

Temperatures at the 60 cm depth were slightly lower generally than those at the 30 cm depth (compare Figs. 2 and 3). This could mean that indeed it is cooler at 60 cm or that there is a lag in daily warming at 60 cm, making 16:15 an inappropriate time for estimating daily mean temperature (see Mrosovsky and Provancha 1989). However, because thermal fluctuations are much reduced at 60 cm, the time of day chosen for readings makes less difference. It is clear that even if the 60-cm values obtained here are a little lower than the daily means, they are still above the pivotal level for much of the season.
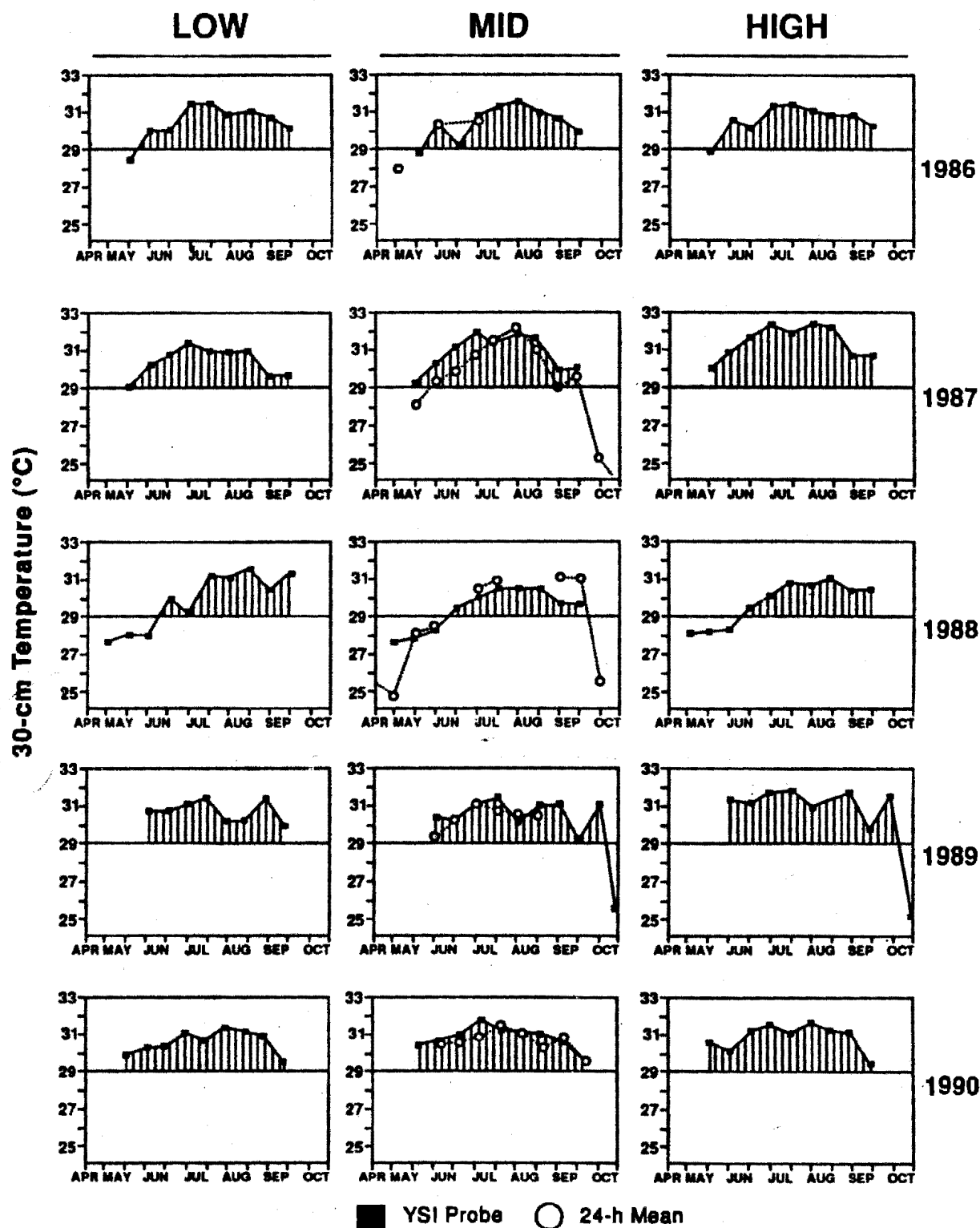
FIG. 2. Temperatures at 30 cm depth for low, mid, and high parts of the beach (squares and solid lines) taken at approximately 16:00 about twice a week with thermistor probes. In addition, on the midbeach, during parts of the season, temperatures were also continuously recorded with a data logger buried at the same depth (circles and broken lines); means for each 24-h period were calculated, and then from these a further mean provided a value for the half-month period. Horizontal lines show the pivotal temperature for loggerhead turtles (Mrosovsky 1988). Hatched area shows times of year when the sand temperature exceeded the pivotal temperature. Scale marks on x-axis closest to start and end of lettering for each month designate first and second half-month bins for that month.

Discussion

A number of sex-ratio studies in reptiles with temperature-dependent sexual differentiation have found biases toward females. When such data are incorporated into tables, meta-analyses, and theoretical formulations, it is important to remember the problems in obtaining valid estimates of equilibrium sex ratios in reptiles. We start here by briefly reviewing some potential sampling biases in these studies, so that our
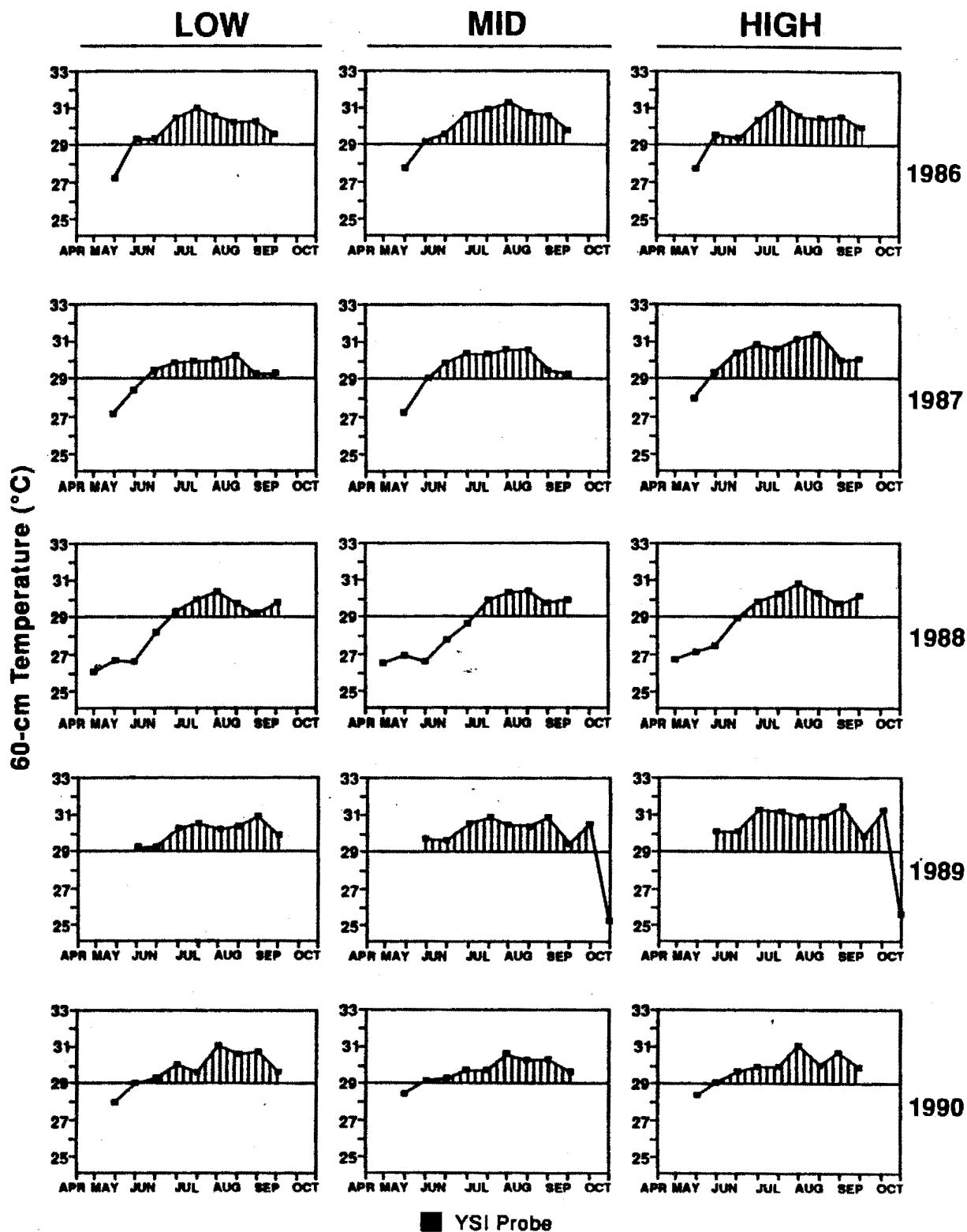
FIG. 3. Temperatures for 60 cm depth. Conventions and details are the same as for Fig. 2; no data loggers were buried at 60 cm.

own figures for loggerhead turtles are not accepted as more than initial estimates, and also so that theorizing in this area is balanced by caution about the difficulties in obtaining a solid data base.

Servan et al. (1989) found that 67% (*n* = 184) of European pond turtles were female. These were mature turtles; sex differences in mortality, susceptibility to being trapped, and other factors affecting sampling cannot be excluded (see Gibbons 1990). One is not, therefore, compelled to agree that "the primary cause of these biases must have been hatchling sex ratio" (Servan et al. 1989). In this discussion we concentrate on studies of hatchlings.

Vogt and Bull (1984) found that 72% of map turtle hatchlings at a Wisconsin site were female. In a cooler year only

55% were female (Bull and Charnov 1988). Nests of small turtles may be harder to find if they are in shaded, male-producing undergrowth. Also, dredging in this river system had created extra open habitat. Artificiality of habitat is also a concern in connection with the 69% female value for hatchling snapping turtles in Ontario (Brooks and Nancekivell 1984). The nesting area was on a man-made embankment (R. J. Brooks, personal communication). The same problem applies to the interpretation of data on northern painted turtles. In 2 years there were 88% (n = 79) and 87% (n = 133) females, but the hatchlings were from nests laid on a relatively bare railway embankment (Schwarzkopf and Brooks 1985).

Spotila et al. (1987) estimated that 67% of green turtles hatching at Tortuguero, Costa Rica, were female, but sampling did not cover a full nesting season (see Mrosovsky and Provancha 1989). Preliminary estimates of a value of about 40% female come from another season in Tortuguero (Horikoshi 1992). About equal numbers (55% female) of each sex of green turtles were produced in Suriname over a nesting season (Mrosovsky et al. 1984a); it is not known if the weather during this year was normal. Hatchlings collected in another year during just a part of the season yielded relatively more females.

Leatherback turtles were also studied in Suriname (Mrosovsky et al. 1984a). In addition to the question of whether the year selected was thermally typical, a further complication arises. Leatherbacks nested unusually late in the year of this study, 1982; they laid more of their eggs than usual in the drier, warmer end of the season. If calculations are based on the nesting distribution for 1982, then 61% of the hatchlings produced were females. But if leatherbacks had nested in 1982 at times when they normally nest, then only 49% would have been females. Time of nesting as well as temperature should be shown to be typical for trustworthy estimates of sex ratio.

In another study of leatherbacks in Michoacan, Mexico, it was estimated that 54% of the hatchlings were females, 32% males, and 14% intersexes (Benabib 1984). However, the sexing was done by examining glycerine-cleared gonads; this technique is not always reliable (Mrosovsky and Benabib 1990).

Other sex ratios worth noting are those for juveniles. If at this stage sex differences in behaviour do not influence the probability of capture, then perhaps juvenile sex ratios reflect primary sex ratios. For green turtles at Heron Reef, Australia, the juvenile ratio was 54% female, n = 145 (Limpus and Reed 1985). Of the immature loggerhead turtles caught along the east coast of the U.S.A., 66% were female, n = 256 (Wibbels et al. 1987; see also Wibbels et al. 1991). These juveniles came from eggs laid before our study began. This suggests that hatchling sex ratios may have been female-biased for more than the 5 years of our study.

· Turning from chelonians to crocodilians, Ferguson and Joanen (1982) collected alligator eggs in Louisiana from natural nests "after 5 weeks of incubation." They then incubated the eggs at 32°C. The procedure was repeated over 4 years. On average, 83.3% of the animals surviving to 1.5 years were female. This method depends on the assumption that the thermosensitive period had passed by the time the eggs were brought into the 32°C incubators. This assumption is not entirely satisfied. In other experiments, alligator eggs were shifted from male-producing (34°C) to female-producing (30°C) temperatures. If this shift occurred after 5 weeks of incubation, then 40% of the hatchlings were female; if it
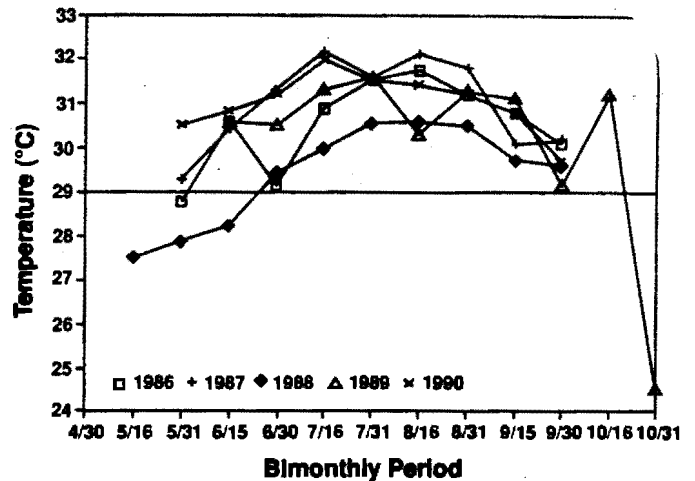

FIG. 4. Comparison of midbeach temperatures at 30 cm depth (thermistor readings at 16:00 taken about twice a week) between different years. The horizontal line shows the pivotal temperature. Dates refer to end of half-month periods.

occurred 1 week later, then only 5% were female (Deeming and Ferguson 1989a). Sex had not been irreversibly determined by the end of week 5, because keeping the eggs for a further week at male-producing temperatures reduced the percentage of females. The data (Deeming and Ferguson 1989a) do not, therefore, support the statement by Ferguson and Joanen (1982) that "sex was determined by the incubation temperature during weeks 2 and 3; thereafter changes in incubation temperature had no effect." Moreover, the temperature used in the laboratory phase of this work, 32°C, was one that gives a sex ratio of 85% female when it prevails throughout incubation (Ferguson and Joanen 1982, 1983). Perhaps the similarity between the sex ratios for the sample brought in from the field (83.3% female) and the sample incubated at 32°C (85% female) is a coincidence, but it would be desirable to learn more about thermal effects after the 5th week of incubation. Even if there is a female bias in the wild, one may still question whether this is an equilibrium value, or relates to expansion of this population after years of excessive hunting (Deeming and Ferguson 1989b).

For Australian freshwater crocodiles the mean percentage of females in 19 clutches from one river was 57 (Webb and Smith 1984). When crocodiles from a number of rivers were caught over 7 weeks following the first hatching, the percentage of females ranged from 39 to 88, with an overall value of 65. However, this figure might have been unduly influenced by samples from particular rivers.

Sex ratios of Nile crocodile hatchlings and embryos collected in the Lake Ngezi area, Zimbabwe, from four clutches in 1979 and four in 1981 were 89 and 91% female, respectively (Hutton 1987). Whether these small samples reflected the proportion of natural nests laid in sunny and shady areas is unclear. In a sample of 80 wild-caught crocodiles of size class greater than hatchlings, 67% were females. However, Lake Ngezi, artificially altered by damming and unusually elevated (1220 m), may not be representative of Nile crocodile habitat.

With the present study on loggerhead turtles, we are confident that the sampling was reasonably fair, both spatially and temporally. There were no great differences between clutches designated for this project and those added retrospectively (Table 1; Mrosovsky and Provancha 1989). Three years of
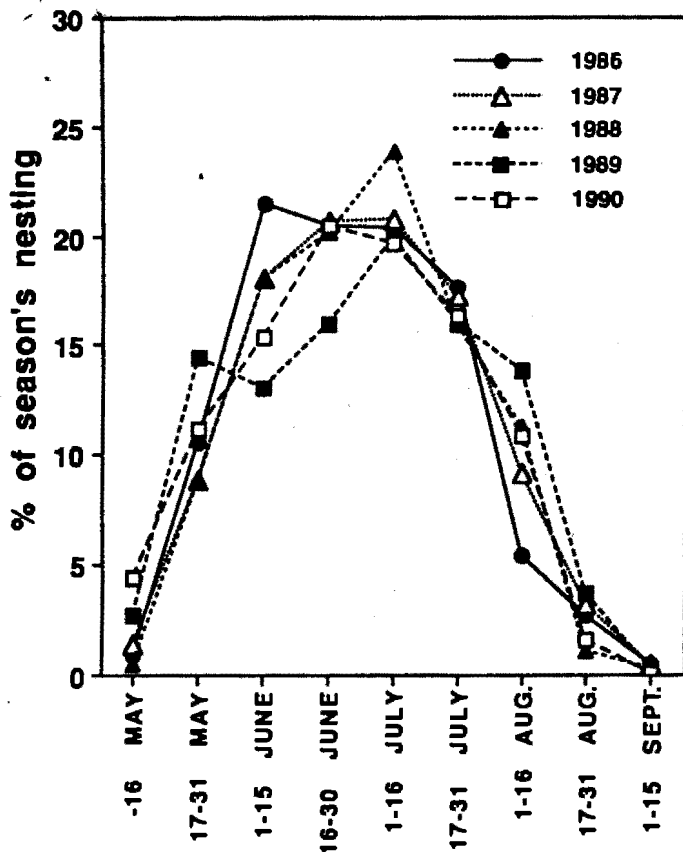
Fig. 5. Distribution of nests (laying dates) over different years expressed as a percentage of the total nests in each season.

sampling hatchlings and 5 years of recording temperatures show that highly skewed ratios do not arise only in occasional years. Moreover, nesting distributions were similar over the 5 years (Fig. 5). However, in 1990 more turtles laid in early May. If the 1988 sex-ratio data (the most "male" of the sampling years) were applied to the 1990 nesting distribution, then the percentage of females could dip below 83 (assuming that all hatchlings from the unsampled ends of the season were males), but this is still a highly skewed value.

Does this female bias represent an equilibrium value? Turtles nesting at Cape Canaveral might be only part of a larger interbreeding population nesting along the southeastern coast of the U.S.A. There might be male-producing areas in the north and female-producing areas in the south (with a relatively even overall ratio). Several points suggest that relatively more males are produced at the more northerly rookeries. Pivotal temperatures for turtles nesting in North Carolina are close to those for turtles nesting in Florida, but incubation times, an index of temperature, are often longer in North Carolina (Mrosovsky 1988). Therefore, it seems inevitable that higher percentages of turtles hatching in North Carolina will be males than in Florida; preliminary data from North Carolina agree with this (W. D. Webster, personal communication). Also, it was estimated that in South Carolina and Georgia, 48–56% of the hatchlings were female, although sampling imperfections make these estimates questionable (Mrosovsky et al. 1984b). The extent of reproductive mixing between Cape Canaveral loggerheads and those nesting farther north is unknown. There are a few documented cases of individuals nesting on different beaches at different times

(e.g., LeBuff 1974). Whether they nest elsewhere or not, females tagged on Florida beaches disperse widely and can travel at least 1500 km (Meylan et al. 1983). However, even if all the U.S. loggerheads are one interbreeding population, there would still be a female bias because 90% of these turtles presently nest in Florida (Murphy and Hopkins 1984). Yet even this does not incontrovertibly demonstrate a female-biased equilibrium sex ratio because it is conceivable that relatively greater numbers nested on the more northerly male-producing beaches in the past than do so today. The overall sex ratio could possibly have been 1:1 before the arrival of people in the U.S.A.

Another way in which disequilibrium might result is if declines in the overall population liberated preferred niches for turtles otherwise forced into marginal patches. Suppose that for embryos incubated in warm sand, fitness is higher for a female than for a male, and that for incubation in cool sand, even though fitness is higher for a male than a female, overall it is lower than in the warmer sand. Then the warmer area is the best patch for producing fitter progeny. Population declines might allow individuals previously forced to use poorer patches (possibly northern areas) to move into unoccupied good patches (a patch might include habitats necessary for feeding and preparatory activities for laying in areas with particular thermal characteristics). The overall sex ratio would then become female biased, until frequency-dependent selection had time to work or until the population recovered. This idea predicts that population differences in sex ratio would be related to the state of the population.

At present there is no evidence for these speculations about how loggerheads might have moved into a disequilibrium state, if indeed they are in such a state. This leads us back to the extreme bias in our sample. The highly female-biased sex ratios found here and in a number of other studies on reptiles pose three major challenges: an empirical challenge, a theoretical challenge, and a challenge for conservation policy.

The empirical task is to sample extensively enough to be confident that hatchling sex ratios are indeed skewed. How many potentially atypical years can follow each other before it can be said that they are not really atypical? The need for projects spanning years, even decades, could perhaps be avoided by combining a solid data base on pivotal temperatures with meteorological records. However, it remains to be shown that air temperatures from weather stations can predict soil temperatures at turtle nest depth on beaches thermally buffered by large water masses. One also needs to know the limits of the breeding unit so that it can be fairly represented in the sample. The present study, like some of the others, goes only some way toward these ideals. More empirical work is worth the effort because if highly skewed sex ratios can be substantiated they will either necessitate elaboration of classical sex-ratio theory, or mean that there are important aspects of the life history or physiology of these reptiles of which we are unaware.

Classical theory predicts that in a population there should be equal investment in each sex (Fisher 1930). For sea turtles this means a primary sex ratio close to 1:1 because the cost of eggs, whatever sex they later produce, is close: egg size is relatively constant, and parental investment ends at laying. If a skewed ratio does occur, this would not necessarily invalidate the theory: it could be that some of the conditions under which this theory applies have not been met (Bull and Charnov 1988). For instance, Fisherian sex ratios require that mating

be random. Perhaps skewed ratios arise because recruits do not join a large random mating pool. Perhaps turtle populations are structured in some way that brings siblings in contact (Mrosovsky 1980). Another possible violation of the assumptions required for Fisherian ratios is that a cytoplasmic factor influences the mother to overproduce daughters; yet another possibility is that the fitness of males and females depends differentially on incubation temperature (Bull and Charnov, 1988). However, for all the possibilities just mentioned, the counterbalancing frequency-dependent effects of producing more offspring of one sex should still be operative. Therefore, for biases as great as 90% female, Fisherian assumptions would have to be violated in a powerful manner. Perhaps also there is some as yet unformulated reason why Fisher's theory might not apply to species susceptible to thermal effects on sex ratio, but this seems unlikely, given work on fish whose phenotypic sex is partly determined by temperature. In captivity, populations of silversides starting with imbalanced sex ratios evolve balanced sex ratios over six generations (Conover and Voorhees 1990).

Nevertheless, the almost unthinkable might also be considered, that Fisherian theory is somehow wrong. Perhaps this is too extreme, but at least it is important that the theory be tested in more varied ways. The more that extreme sex ratios are found in species lacking sex chromosomes, the more it becomes necessary to look into the matter because when 1:1 ratios are found in mammals, for instance, it can always be argued that this is the inevitable result of having XX−YY chromosomes. A counterargument is that such "mechanisms as XY and X0 sex determination (where X and Y represent sex chromosomes and 0 denotes the absence of a chromosome) are not to be viewed as some inevitable result of chromosome mechanics but rather as specialized devices favored by natural selection because they generate 50/50 sex ratios with a minimum of complication" (Wilson 1975). But even if this were true, why then have so many reptiles failed to evolve chromosomal systems ensuring 50/50 ratios with the minimum of complication? In any case, equal investment in the sexes should apply to reptiles. So far, although the evidence against equal investment is not, as discussed above, definitive or incontrovertible, there is precious little evidence in support of Fisherian ratios in reptiles with thermally determined sex ratios. The empirical and the theoretical challenges of these highly skewed ratios are, therefore, closely related.

The conservation challenge concerns the effects of possible global warming (Pool 1991). In Suriname, even a 2°C warming of the sand would put temperatures in the female-producing range for the entire present nesting season of green and leatherback turtles (Mrosovsky et al. 1984a). Perhaps extinction would follow. Such fears have been dismissed by Deeming and Ferguson (1989b), who assert: "Much rubbish has been said and written about skewed sex ratios among animals with TSD [temperature dependent sex determination]. It is unlikely that their sex ratio would be skewed too far because these animals will select different nest sites and rapidly adapt to the changed climate." The possibility of shifts in nest-site preference has been considered before (Mrosovsky 1984), but at least for sea turtles, it is debatable whether they can change fast enough. Some species show strong nest-site fidelity: documented exceptions of individuals nesting on widely separated beaches are rare (e.g., Le Gall and Hughes 1987). Maturation time of sea turtles is long, >30 years according to some estimates (Balazs 1981). If nest-site prefer-

ences have strong genetic components, there may no enough time to adapt to rapid changes in climate. Possi natural selection might be able to exert pressure on the tim of nesting (see variability in Fig. 5), but again a long maturation period could be a problem.

A different suggestion that could calm fears about global warming is that latitudinal differences in pivotal temperature might be influenced by an individual's thermal history, and that therefore females in a climate subject to the greenhouse effect might lay clutches with higher pivotal temperatures (Davenport 1989). However, there is as yet little evidence for latitudinal differences in pivotal temperatures (review in Mrosovsky 1988), and no data exist on phenotypic contributions to pivotal temperatures. Speculation about changes in pivotal levels or in behaviour should be treated with caution.

Too little is known about nest-site selection to be confident that it is flexible enough to cope with global warming. There may be constraints on nest-site selection other than those related to sex ratio. It might seem simple for sea turtles to move into thermally different microhabitats; however, if, for example, loggerheads nested higher up on the beach, that might increase the chances of roots invading the clutch, and perhaps also of certain predators devouring the eggs. Hatchlings emerging in the undergrowth may have more trouble reaching the sea (Mrosovsky 1983). If females nested lower down the beach, their eggs might often become flooded. Pressures on the survival of eggs and hatchlings might limit flexibility in nest-site selection. Altered nest-site selection probably requires other adaptations that may or may not be able to evolve fast enough. For the sake of the reptiles, we hope that Deeming and Ferguson's (1989b) optimism will be justified. In case it is not, it would be prudent to formulate contingency plans. Demonstrations of sex-ratio evolution in faster maturing species do not make it safe to assume that turtles will survive rapid global warming. Indeed, one conceivable explanation of the skewed sex ratios in our study is that the climate at Cape Canaveral has already started to change, and that the sand temperatures for 1986−1990 were above the average for the last few hundred years.

Acknowledgements

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